

New Evanioid Wasps from the Cenomanian of Myanmar (Hymenoptera: Othniodellithidae, Aulacidae), with a Summary of Family-Group Names among Evanioidea

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ABSTRACT

Three new evanioid wasps (Euhymenoptera: Evanioidea) are described and figured from individuals preserved in mid-Cretaceous (earliest Cenomanian) amber from northern Myanmar. The new species represent the families Othniodellithidae and Aulacidae, both previously recorded from Burmese amber. *Xenodellitha preta*, new genus and species, is the second othniodellithid wasp and the diagnosis of the family is slightly emended in order to accommodate this species. The subfamily Hyptiogastritinae (Aulacidae) is expanded to include *Protofoenus* Cockerell and a third genus from Burmese amber. *Archeofoenus tartaricus*, new genus and species, is the third known species of the extinct aulacid subfamily Hyptiogastritinae, differing from *Hyptiogastrites electrinus* Cockerell in the low position of the discal cell and the open subdiscal cell in the forewing, and from *Protofoenus swinhoei* Cockerell in the form of the head and mandible, coloration, and forewing venational details. Together, *Archeofoenus* and *Protofoenus* are placed in Archeofoenini, new tribe. The last species is similar to the genus *Electrofoenus* Cockerell, and together they are classified in Electrofoenini among the Aulacidae. *Electrofoenops diminuta*, new genus and species, is distinguished from *Electrofoenus* on the basis of wing venation. The significance of these taxa is briefly discussed and a summary of available family-group names among Evanioidea is appended.

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INTRODUCTION

With their characteristic articulation of the metasoma high on the propodeum and well above the metacoxae, wasps of the superfamily Evanioidea are among the more easily recognized groups of the nonaculeate Euhymenoptera. These wasps are largely predators or ectoparasites of roaches or aculeate wasps and bees (Huben, 1995; Jennings and Austin, 2004), but primitively include parasitoids of wood-boring beetles and wood wasps (Jennings and Austin, 2004). Today Evanioidea comprises approximately 2200 species (Huber, 2009; Engel and Krombein, 2012; Aguiar et al., 2013), and depending on the classification adopted, these are arranged in two or three families. Since the works of Bischoff (1927), Hedicke (1930, 1939a, 1939b, 1939c), and Crosskey (1951, 1962), the most consistent classification considers the superfamily to comprise three extant families—Aulacidae, Gasteruptiidae, and Evaniidae (e.g., Mason, 1993; Grimaldi and Engel, 2005; Sharkey et al., 2012). The monophyly of evanioids is abundantly supported in analyses of morphological and molecular data sources (e.g., Downton and Austin, 1994; Downton et al., 1997; Vilhelmsen et al., 2010; Sharkey et al., 2012; Payne et al., 2013), and they are also one of the few superfamilies for which there have been comparatively comprehensive modern phylogenetic studies and revisions (e.g., Aulacidae [Jennings and Austin, 2000; Smith, 2001; Turrisi, 2006, 2007, 2014; Turrisi et al., 2009; Turrisi and Madl, 2013], Gasteruptiidae [Jennings and Austin, 2002; Macedo, 2009, 2011; Zhao et al., 2012; Achterberg and Talebi, 2014], Evaniidae [Deans and Huben, 2003; Deans, 2005; Deans et al., 2006; Kawada and Azevedo, 2007; Mullins et al., 2012]).

Fossil Evanioidea are not uncommon, and there have been several aulacids and evaniids described from Eocene and Miocene deposits found in Europe, Mexico, and the Dominican Republic (Brues, 1933; Nel et al., 2002a, 2002b, 2004; Sawoniewicz and Kupryjanowicz, 2003; Jennings and Krogmann, 2009; Jennings et al., 2012, 2013a; personal obs.). More interestingly, these same families, or stem groups to these taxa, are similarly documented from Cretaceous sediments in Central Asia, Europe, and southern Africa (e.g., Zhang et al., 2007; Rasnitsyn and Brothers, 2007), as well as fossiliferous resins from the same period (table 1) (e.g., Cockerell, 1917a; Rasnitsyn, 1975; Basibuyuk et al., 2002; Jennings et al., 2004, 2013b; Deans et al., 2004; Engel, 2006; Peñalver et al., 2010). The Cretaceous also includes a few genera that are considered to be basal to crown-group Gasteruptiidae (Rasnitsyn, 1991; Engel and Wang, 2016). Beyond the bounds of these familiar families, the Mesozoic includes an even greater diversity of genera that fall well outside the extant families, regardless of how broadly circumscribed, and represent a grade of extinct families (e.g., Rasnitsyn, 1972, 1975; Zhang and Rasnitsyn, 2004, 2007, 2008; Engel, 2013; Li et al., 2015; Engel et al., 2016a). While a few of these families are rather generalized, such as Praeaulacidae relative to all evanioids, and Anomopterellidae in comparison to Neoevanioides (Rasnitsyn, 1972, 1975; Zhang and Rasnitsyn, 2008), others are remarkably specialized in their own right. For example, the Nevaniidae are noteworthy for the presence of a bipetiolate metasoma (Zhang and Rasnitsyn, 2007), while the Othniodellithidae have enlarged cephalic horns and large, squared mandibles (Engel et al., 2016a).

Described here are three new species of mid-Cretaceous evanioid wasps, representing the families Othniodellithidae and Aulacidae. These species are among the earliest of amber-pre-

TABLE 1. Cretaceous amber Evanioidea arranged by amber deposit, with familial placement indicated.

LEBANON (APTIAN)	
<i>Cretevania cyrtocerca</i> (Deans in Deans et al., 2004)	Evaniidae
<i>Lebanevania azari</i> Basibuyuk and Rasnitsyn in Basibuyuk et al., 2002	Evaniidae
<i>Protoparevania lourothi</i> Deans in Deans et al., 2004	Evaniidae
SPAIN (ALBIAN)	
<i>Cretevania alcalai</i> Peñalver et al., 2010	Evaniidae
<i>Cretevania alonsoi</i> Peñalver et al., 2010	Evaniidae
<i>Cretevania montoyai</i> Peñalver et al., 2010	Evaniidae
<i>Cretevania rubusensis</i> Peñalver et al., 2010	Evaniidae
<i>Cretevania sopraensis</i> Pérez-de la Fuente et al., 2012	Evaniidae
<i>Iberoevania roblesi</i> Peñalver et al., 2010	Evaniidae
MYANMAR (CENOMANIAN)	
<i>Archeofoenus tartaricus</i> , n. gen., n. sp.	Aulacidae
<i>Cretevania bechlyi</i> Jennings et al., 2013b	Evaniidae
<i>Electrofoenops diminuta</i> , n. gen., n. sp.	Aulacidae
<i>Electrofoenus gracilipes</i> Cockerell, 1917b	Aulacidae
<i>Habraulacus zhaoi</i> Li et al., 2015	Praeaulacidae
<i>Hypselogastrion simplex</i> Engel and Wang, 2016	Gasteruptiidae
<i>Hyptiogastrites electrinus</i> Cockerell, 1917a	Aulacidae
<i>Mesevania swinhoei</i> Basibuyuk and Rasnitsyn in Basibuyuk et al., 2000a	Evaniidae
<i>Othniodellitha mantichora</i> Engel and Huang in Engel et al., 2016a	Othniodellithidae
<i>Protofoenus swinhoei</i> Cockerell, 1917a	Aulacidae
<i>Sorellevania deansi</i> Engel, 2006	Evaniidae
<i>Xenodellitha preta</i> , n. gen., n. sp.	Othniodellithidae
AGAPA (CENOMANIAN)	
<i>Cretevania minuta</i> Rasnitsyn, 1975	Evaniidae
NEW JERSEY (TURONIAN)	
<i>Electrobaissa omega</i> Engel, 2013	Baissidae
<i>Grimaldivania ackermani</i> Basibuyuk et al., 2000b	Evaniidae
<i>Grimaldivania mckimorum</i> Engel, 2006	Evaniidae
<i>Newjersevania casei</i> Basibuyuk et al., 2000b	Evaniidae
<i>Newjersevania nascimbenei</i> Basibuyuk et al., 2000b	Evaniidae
TAIMYR (SANTONIAN)	
<i>Cretevania major</i> Rasnitsyn, 1975	Evaniidae
<i>Cretevania minor</i> Rasnitsyn, 1975	Evaniidae

served Evanioidea, predated only by those in Lebanese (Basibuyuk et al., 2002; Deans et al., 2004) and Spanish amber (Peñalver et al., 2010; Pérez-de la Fuente et al., 2012). These species are described and their significance briefly discussed. In addition, the opportunity is taken to append an account of family-group names presently available within the Evanioidea (appendix).

MATERIAL AND METHODS

All of the material discussed here is deposited in the amber fossil collection of the Division of Invertebrate Zoology, American Museum of Natural History, New York. Two specimens are from the James S. Zigras Collection, which through an agreement with the AMNH will be permanently deposited there. Three evanioid wasps were identified in comparatively clear pieces of amber from the State of Kachin in northern Myanmar. Prior to study, each piece was trimmed and polished, and one (Bu-096) was embedded within a small block of epoxy using the procedures outlined by Nascimbene and Silverstein (2000). The location, age, geological setting, and biotic diversity of the amber from northern Myanmar has been reviewed by Grimaldi et al. (2002), Cruickshank and Ko (2003), Ross et al. (2010), and Shi et al. (2012). The amber has been generally dated to the earliest Cenomanian, near the Albian boundary, with radiometric dates from surrounding zircons suggesting an absolute age estimate near 98 Ma (Shi et al., 2012). Burmese amber is currently the most abundant source of Mesozoic amber inclusions, and includes the greatest diversity of arthropods discovered to date (Grimaldi et al., 2002; Ross et al., 2010). The significance of Burmese amber for understanding Cretaceous biotic evolution cannot be overestimated, and even recently these mines have revealed the earliest Palpigradi (Engel et al., 2016b), Neophasmatodea (Engel et al., 2016c), diverse ants and termites (Barden and Grimaldi, 2016; Engel et al., 2016d; Perrichot et al., 2016), as well as amber-preserved vertebrates within Squamata (Daza et al., 2016).

Microphotographs were executed using a Canon EOS 7D digital camera attached to an Infinity K-2 long-distance microscope lens, and illuminated by a coordinated Xenon-flash system. Final images were made by combining consecutive photographs taken at successive focal planes using CombineZP software. Measurements of specimens were taken with the aid of an ocular reticle on an Olympus SZX12 stereomicroscope. The classification of Evanioidea followed is that outlined by Engel et al. (2016a) and Engel and Wang (2016) (table 2). General morphological terminology largely follows that of Huber and Sharkey (1993) and Sharkey and Wharton (1997) in certain annotations for wing vein nomenclature.

SYSTEMATIC PALEONTOLOGY

Superfamily Evanioidea Latreille, 1802

Family Othniodellithidae Engel and Huang in Engel et al., 2016a

Othniodellithidae Engel and Huang in Engel et al., 2016a: 123. Type genus: *Othniodellitha* Engel and Huang in Engel et al., 2016a.

TABLE 2. Hierarchical, suprageneric classification of Evanioidea. Dates and citations for names provided in appendix.

Superfamily Evanioidea Latreille	Family †Praeaulacidae Rasnitsyn
	Subfamily †Praeaulacinae Rasnitsyn
	Subfamily †Cretocleistogastrinae Rasnitsyn
	Family †Nevaniidae Zhang and Rasnitsyn
	Family †Andreneliidae ¹ Rasnitsyn and Martínez-Delclòs
	Family †Othniodellithidae Engel and Huang
Neoevanioides Engel	Family †Anomopterellidae Rasnitsyn
Aulaciformes Grimaldi and Engel	Family †Baissidae Rasnitsyn
Euaulacides Engel	Family Gasteruptiidae Ashmead
	Subfamily †Hypselogastrinae Engel
	Subfamily †Kotujellitinae Rasnitsyn
	Subfamily Hyptiogastrinae Crosskey
	Subfamily Gasteruptiinae Ashmead
	Family Aulacidae Shuckard
	Subfamily †Hyptiogastritinae ² Engel
	Tribe †Archeofoenini, n. trib.
	Tribe †Hyptiogastritini Engel
	Subfamily Aulacinae Shuckard
	Tribe †Electrofoenini Cockerell
	Tribe Aulacini Shuckard
Evaniiformes Grimaldi and Engel	
	Family Evaniidae Latreille

¹ This group is little understood and the available material is partial (Rasnitsyn and Martínez-Delclòs, 2000). It may be a stem-group evaniid and therefore best considered within that family, but there are otherwise notable plesiomorphies that suggest it could be a bizarre anomopterellid or even a praeaulacid of some kind. For the time being I have considered it as basal among Evanioidea pending the discovery of more complete material.

² The two tribes presently included may form a grade and might require future elevation as separate subfamilies. Pending a thorough cladistic analysis of living and fossil Aulaciformes, I have conservatively retained them within the traditional concept of Hyptiogastritinae (sensu Engel, 2006).

DIAGNOSIS (emended from Engel et al., 2016a): Small wasps (approximately 4–5 mm in length), integument of head and mesosoma not transversely striate or rugose (variously with transverse striae in Praeaulacidae, Andreneliidae, and Nevaniidae: refer to Rasnitsyn, 1972, 1975; Zhang and Rasnitsyn, 2008); head comparatively large, with pronounced cephalic horn projecting from frons and well in front of face in profile (figs. 1, 2A), with toruli situated on lateral sloping surfaces of horn; antenna filiform, with 20–21 flagellomeres; scape relatively long; flagellomeres longer than wide, tapering in length toward apex of flagellum. Clypeus with base indistinct owing to absence of epistomal sulcus, thus clypeus and frons apparently fused; clypeus with strong, elevated, medial ridge projecting apically beyond lower margin of face as narrowly rounded, triangular process between mandibles. Mandibles massive, blocky, almost square shaped, with series of teeth along margin (distinct in *Xenodellitha preta*, n. sp., below; blunt [possibly worn?] in *Othniodellitha mantichora* Engel and Huang [Engel et al., 2016a]), and with large, pointed apical tooth (greatly overlapping other mandible in *O. mantichora*). Maxillary palpus elongate, with four to five palpomeres (clearly five palpomeres in *X. preta*; *O.*

mantichora apparently with four but not as clear in holotype [Engel et al., 2016a]), basal palpomere slightly longer than wide (*O. mantichora*) or about 2.5 times longer than wide (*X. preta*), remaining palpomeres thin and greatly elongate such that palpus is distinctly longer than compound eye length. Ocelli present, positioned close together on top of vertex and above upper tangent of compound eyes; compound eyes large, semicircular to ovoid, with inner margins slightly convergent to slightly divergent below; occipital carina complete, less prominent mediodorsally, but present. Mesosoma somewhat laterally compressed, narrower than head; pronotum comparatively long medially, creating a short neck; propleurae not projected forward beyond pronotum; mesoscutum with faint median sulcus, notauli weak but complete; mesoscutal transverse sulcus present; mesopleuron with weak oblique depression (apparently for reception of midleg when appressed to body); propodeum with prominent dorsal surface, twice as long as metanotum; articulation of metasoma high on propodeum, well above metacoxae and at angle between dorsal and posterior surfaces of propodeum. Legs long and slender; pro- and mesotrochantelli largely fused into base of associated femora but discernible, metatrochantellus distinct, slanted; tarsi pentamerous; tibial spur formula 1-2-2; pretarsal claws long, thin, comparatively straight except at apex, with minute subapical tooth, arolium small. Forewing venation comparatively complete, with rs-m crossveins weakened and 2m-cu nebulous (*X. preta*, below) or lacking (*O. mantichora*); basal vein forking distad midlength of Sc+R; 1cu-a confluent to slightly distad basal vein; marginal cell large, wide near tangent with apex of pterostigma and elongate, nearly reaching to wing apex. Hind-wing venation complete except lacking C, lacking jugal lobe. Metasoma petiolate, with gaster (i.e., metasomal segments posterior to petiole) cylindrical elongate (*X. preta*) or laterally compressed and ovoid (*O. mantichora*), articulation with mesosoma high, well above metacoxae, articulation well separated from metanotum, anterior petiolar width less than length of dorsal-facing surface of propodeum; first metasomal segment tubular, with tergum I and sternum I fused, remaining metasomal segments (those comprising the gaster); ovipositor and sheaths moderately long, extending beyond metasomal apex, approximately two-thirds gaster length (known only from *O. mantichora*: Engel et al., 2016a).

COMMENTS: The diagnosis of the family is here emended to accommodate a new species from Burmese amber (described below). In particular, the number of flagellomeres, proportion of head elements (e.g., genal breadth, malar length), details of wing venation, and form of the metasoma all require some expansion of the familial concept. Unfortunately, the new taxon does not provide any insights into the possible function of the peculiar cephalic horn that makes these wasps so distinctive among other basal evanioids.

Key to Genera of Othniodellithidae

1. Flagellum with 20 flagellomeres; scape about 2.6× as long as wide; gena narrower than compound eye; forewing basal vein confluent with 1cu-a; 2cu-a present; 2m-cu nebulous; metasoma beyond petiole cylindrical; apical tooth of mandible slightly projecting *Xenodellitha*, n. gen.

- Flagellum with 21 flagellomeres; scale about 5.6× as long as wide; gena broader than compound eye; forewing basal vein distal of 1cu-a; 2cu-a absent; 2m-cu absent; metasoma beyond petiole ovoid; apical tooth of mandible greatly projecting and overlapping opposing mandible *Othniodellitha* Engel and Huang

***Xenodellitha*, new genus**

TYPE SPECIES: *Xenodellitha preta*, new species.

DIAGNOSIS: Similar to *Othniodellitha* Engel and Huang (in Engel et al., 2016a) in those ways outlined in familial diagnosis (above) but may be distinguished by following combination of traits: flagellum with 20 flagellomeres; scape about 2.6× as long as wide; apical tooth of mandible slightly projecting; gena narrower than compound eye; forewing with 1cu-a confluent with 1M, 2m-cu nebulous, 2cu-a present, and third submarginal cell longer than second submarginal cell; metasoma beyond petiole cylindrical.

ETYMOLOGY: The new generic name is a combination of the Greek words, *xenos* (“stranger”) and *dellithos* (“a kind of wasp”). The gender of the name is feminine.

***Xenodellitha preta*, new species**

Figures 1–2

DIAGNOSIS: As for genus (above).

DESCRIPTION: Total length as preserved (excluding antennae, and to apparent apex of metasomal segment VI as specimen is not preserved beyond that point) 4.15 mm; forewing length 2.55 mm; integument largely dark brown (where not augmented by preservation), largely glabrous; integument without pronounced sculpturing or punctation, largely finely imbricate, except propodeum, which is coarsely and strongly areolate; wings clear and hyaline, veins brown to light brown in preserved color.

Head perhaps slightly longer than wide (directly frontal view not possible as preserved); gena narrow, tapering in width from upper to lower tangent of compound eye, narrower than compound eye, genal width at about midlength 0.18 mm; short, narrow malar space separating mandibular base from lower border of compound eye, with space much shorter than basal mandibular width; compound eye ovoid with lower border comparatively flattened, without circumocular carina, inner margins apparently slightly diverging ventrally, compound eye length 0.44 mm, width 0.29 mm (best observed on left side of head); ocelli large, arranged in small triangle on top of vertex above compound eyes and immediately before facial prominence, ocelli separated by approximately their diameter and from posterior border of head by slightly less than twice their diameter. Prominent facial horn projecting to length of 0.29 mm in profile, extending well in front of compound eyes, apex with blunt, upper transverse ridge paralleled by similar lower ridge (fig. 2B). Antennal toruli broadly separated by facial prominence, situated on lateral sloping surfaces of horn such that they open dorsolaterally and sit in front of compound eyes (fig. 2B); scape longer than wide, length about 2.6× width, length 0.26 mm, maximum width 0.10 mm; pedicel

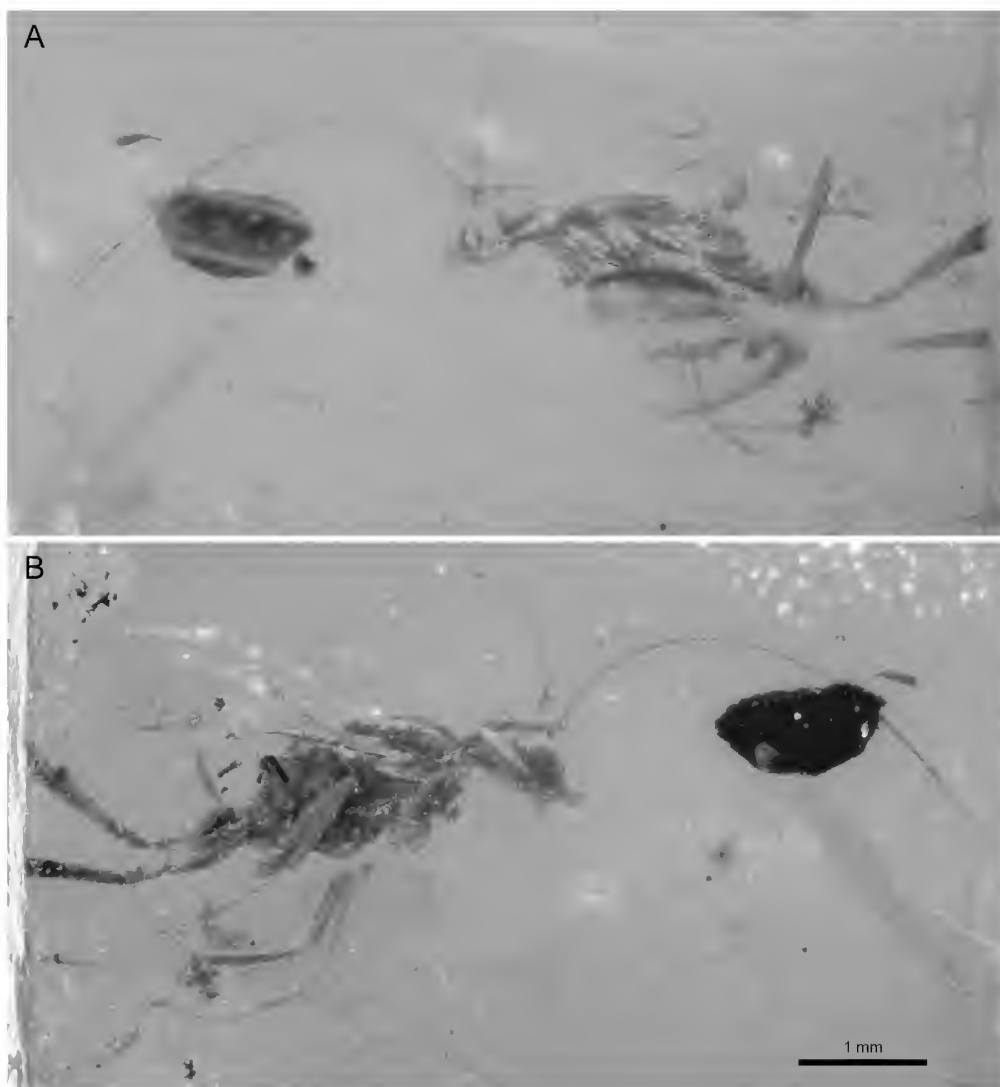


FIGURE 1. Microphotographs of holotype (AMNH Bu-096) of *Xenodellitha preta*, new genus and species, in mid-Cretaceous amber from northern Myanmar (to the same scale). **A.** Left lateral view. **B.** Right lateral view.

about $1.6\times$ as long as wide; flagellomeres each longer than wide, flagellum tapering gradually in length and slightly in width toward apex; first flagellomere longest, about as long as scape. Clypeal base indistinct from frons, with distinct medial longitudinal ridge, ridge extending basally upward to lower origin of facial horn and apically projecting as small triangular prominence between mandibles (fig. 2B). Mandible large, square in frontal view, with straight outer and apical margins, margins meeting at rounded orthogonal outer angle; inner margin with at least three teeth and with one longer, pointed apical tooth (fig. 2B).

Mesosoma laterally compressed, longer than high, length 1.63 mm, maximum height 1.05 mm; pronotum prominent, with poorly defined, raised posterior surface, anterior medial sur-

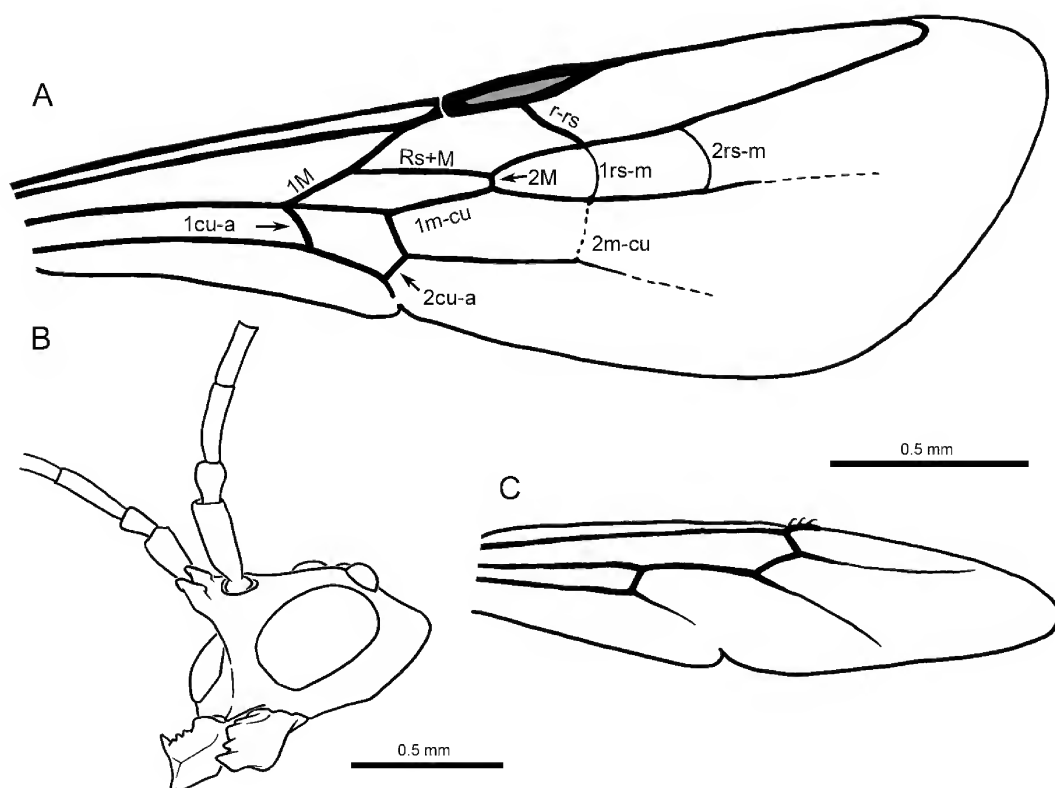


FIGURE 2. Morphological details of holotype (AMNH Bu-096) of *Xenodellitha preta*, new genus and species (wings to the same scale). **A.** Forewing, with pertinent veins labeled. **B.** Head in oblique view. **C.** Hind wing.

face apparently slightly longer than wide and extending forward as short neck, lateral surfaces large and slightly depressed, lateral surface with weak row of areolae bordering mesepisternum; propleura long but not projecting anterior to pronotum; mesoscutum with faint medial line and weak notauli, notauli reaching to transverse sulcus but not meeting sulcus, mesoscutal length 0.56 mm; mesoscutellum arched in profile, medial length 0.31 mm; mesopleuron with oblique depression and small, single row of weak areolae demarcating border with pronotal lateral surface, and even weaker row of areolae along border with metepisternum; metanotum subvertical, short, length 0.11 mm; propodeum coarsely and strongly areolate, with prominent dorsal surface, dorsal length (between metanotum and articulation with metasomal petiole) 0.23 mm. Legs long, with slender podites (hind legs broken at amber's surface; not preserved beyond about basal 0.5–0.75× of metafemoral length in holotype). Forewing (fig. 2B) with costal space apically about as broad as pterostigma; pterostigma much longer than wide, tapering gradually in width in apical half to acute apex, margin inside marginal cell slightly convex; basal vein M+Cu forking distad midlength of Sc+R, 1M straight, forming faint angle at junction with 1Rs, slightly longer than 1Rs; 1Rs originating basal to pterostigma (at distance less than its length but slightly more than basal pterostigmal width); Rs+M straight, forking at

about tangent with pterostigmal basal one-quarter length; 2Rs greatly longer than 2M; 2M exceedingly short and directed posteriorly to meet 1m-cu; 3M longitudinal and extending out toward wing apex; 2Rs largely straight, without kink or rudiment of crossvein; r-rs originating at about pterostigmal midlength, sinuous, elongate, about as long as 2Rs; marginal cell broad, greatest anteroposterior width near tangent of pterostigmal apex, elongate, separated from wing apex by distance less than that of length of pterostigma, with Rs (3Rs+4Rs) comparatively straight for majority of marginal cell length; two rs-m crossveins present, both distinctly weaker and thinner than surrounding veins (but not nebulous), both arched; second submarginal cell with nearly obsolescent anterior border along Rs, posterior border shorter than posterior border of third submarginal cell; third submarginal cell longer than second submarginal cell; discal (discoidal) cell almost forming strongly slanted rhomboid (not distinctly pentagonal owing to exceptionally short 2M), 1m-cu straight, slightly longer than 1Cu; 1cu-a confluent with 1M; 2m-cu nebulous; 2cu-a present and demarcating subdiscal (subdiscoidal) cell. Hind wing with venation largely complete (fig. 2C) except lacking C; R with three distal hamuli, vein terminating immediately beyond hamuli, not meeting Rs apically; rs-m oblique, longer than 1Rs, much shorter than first 1M; Cu+cu-a present, nearly orthogonal to M+Cu; jugal lobe lacking.

Metasoma with first segment forming tubular petiole, petiole length 0.54 mm, narrower basally, basal width at articulation with mesosoma 0.06 mm, becoming thicker at juncture with remainder of metasoma, apical width 0.16 mm, tergum I and sternum I fused without apparent indication of individual sclerites; metasomal segments posterior to petiole not compressed laterally, roughly cylindrical (fig. 1), length as preserved 1.75 mm (metasoma is largely cleared and broken at amber's surface), gradually and slightly tapering in height from segment II to segment VI, maximum height 0.73 mm.

HOLOTYPE: Sex uncertain, possibly male (fig. 1), AMNH Bu-096; Cretaceous amber (Cenomanian), Myanmar, Kachin, Tanai Village on Ledo road 105 km NW of Myitkyna; deposited in the Division of Invertebrate Zoology, American Museum of Natural History, New York.

ETYMOLOGY: The specific epithet is taken from the Classical Sanskrit, *preta*, referring to the spirit of the dead; *pretas* suffered from poor karma in this life, becoming bizarre and starved in the afterlife. The name is treated as a noun in apposition.

Clade Aulaciformes Grimaldi and Engel, 2005

Family Aulacidae Shuckard, 1841

Subfamily Hyptiogastritinae Engel, 2006

Hyptiogastritinae Engel, 2006: 454. Type genus: *Hyptiogastrites* Cockerell, 1917a.

DIAGNOSIS: This extinct subfamily is distinguished from Aulacinae by presence of complete occipital carina, and forewing crossveins 1rs-m, 2rs-m, and 2m-cu absent.

COMMENTS: Previously the subfamily had been considered to consist of only the type genus, but it now seems apparent that the genus *Protofoenus* Cockerell, 1917a, also described from Burmese amber (Cockerell, 1917a), should also be included among the Hyptiogastritinae.

The discovery of a new taxon similar to *Protofoenus* that clearly is more properly grouped among hyptiogastritines tends to indicate that Cockerell's genus is a basal aulacid rather than a gasteruptiid (Foeninæ by his attribution²). This was already clear from the short and broad female metasoma (elongate in Gasteruptiidae), simple metatibia (clavate in Gasteruptiinae and Hyptiogastrinae), nonplicate forewings (plicate at rest in Gasteruptiidae), and comparatively straight course of 3Rs (3Rs is bent anteriorly at about midlength in Gasteruptiinae and Hyptiogastrinae). The discal cell shifted posteriorly and below the level of M+Cu led Cockerell (1917a) to align his fossil with *Gasteruption* Latreille, 1796. His description, while brief, is sufficient to determine its remarkable similarity to the new species presented here, and they are both clearly aulacids. A detailed account of *Hyptiogastrites electrinus* Cockerell, 1917a is provided by Jennings et al. (2004).

Key to Genera of Hyptiogastritinae

- 1.Forewing with discal cell below level of M+Cu (i.e., 1Rs+M forming node with 1Rs, M+Cu, and 1Cu, and with 1M absent) (Fig. 4A); integument with areas of yellow maculation; moderate-sized wasps, approximately 4.5–5 mm in length [Archeofoenini, new tribe] . . . 2
—Forewing with discal cell above level of M+Cu (i.e., 1M present, with 1Rs+M arising from “basal vein” and 1Cu in line with M+Cu); integument dark brown to black, without areas of maculation; small wasps, less than 4 mm in length [tribe Hyptiogastritini Engel]
..... *Hyptiogastrites* Cockerell
- 2.Compound eye large; mandible bidentate; forewing membrane uniformly clear; forewing 2Rs+M and 2Rs weakly angled, 2Rs subequal to 2Rs+M, r-rs equal to 2Rs, and 2M+Cu entirely absent; gena dark brown to black; metafemur dark brown except yellow at apex; metatibia yellow except at extreme apex and on majority of inner surface dark brown . . .
.....*Archeofoenus*, n. gen.
- Compound eye small; mandible simple; forewing membrane infumate in apical half; forewing 2Rs+M and 2Rs distinctly angled, 2Rs shorter than 2Rs+M, r-rs longer than 2Rs, and minute 2M+Cu present (i.e., 1Rs slightly basad 1Cu_a as figured by Cockerell, 1917b); gena entirely yellow; metafemur yellow except black at base; metatibia yellow except black at apex
.....*Protofoenus* Cockerell

Archeofoenini, new tribe

TYPE GENUS: *Archeofoenus*, new genus.

DIAGNOSIS: Forewing with discal cell below level of M+Cu (in this regard resembling many Gasteruptioninae, but otherwise differs in typical gasteruptioniid traits); 1Rs+M forming node with

² In the classificatory system used in Cockerell's accounts of Burmese amber evanioids (Cockerell, 1917a, 1917b) he considered all to belong to Evaniidae, with the subfamilies Evaniinae, Aulacinae, and Foeninae corresponding to the modern Evaniidae, Aulacidae, and Gasteruptionidae, respectively.

1Rs, M+Cu, and 1Cu; 1M absent. Integument with distinct areas of yellow maculation; mesoscutum without transverse carinae or striae of any kind, instead largely smooth to imbricate.

INCLUDED GENERA: *Archeofoenus*, new genus (described below), and *Protofoenus*, both in Cenomanian amber from northern Myanmar.

Archeofoenus, new genus

TYPE SPECIES: *Archeofoenus tartaricus*, new species.

DIAGNOSIS: The new genus is similar to *Protofoenus* but differs in the large compound eye that encompasses the majority of the length of the head in profile (with a short malar space); the broadly bidentate mandible (with prominent, pointed, triangular subapical tooth as long as apical tooth); the uniformly clear wing membranes (without any indication of infuscation) (fig. 3); forewing 2Rs subequal to 2Rs+M, r-rs equal to 2Rs, 2Rs+M and 2Rs weakly angled (nearly forming a straight line), and 2M+Cu entirely absent (fig. 4A); the gena dark brown to black (without any indication of maculation); the metafemur dark brown except yellow at apex (rather than yellow along the majority of its length); and the metatibia yellow except at its extreme apex and on the majority of its inner surface dark brown. In addition, the genus is noteworthy for the broadly rounded profile of the anterior border of the mesoscutum, which is itself raised high above the pronotal posterior border, and the Y-shaped notauli.

ETYMOLOGY: The new generic name is a combination of the Greek, *arche* ("beginning") and *Foenus* Fabricius, an early generic name among the Evanioidea. The gender of the name is masculine.

Archeofoenus tartaricus, new species

Figures 3–5

DIAGNOSIS: As for genus (above).

DESCRIPTION: ♀: Total length as preserved (excluding antennae and ovipositor) 4.80 mm; forewing length 3.25 mm; dark brown to nearly black preserved colors, except yellow as follows: on profemur except basally and apically, protibia except inner surface, apical half of mesofemur, mesotibia except apical half of inner surface, apex of metafemur, metatibia except at extreme apex and majority of inner surface; integument with minute, fine, decumbent setae, such setae particularly numerous on mesoscutum, mesoscutellum, legs, and metasoma; integument largely without pronounced sculpturing or punctation except faintly and finely imbricate (mesoscutum, in particular, not transversely carinate or striate, with rounded anterior lip); metasoma faintly imbricate (metasoma is partially distorted, i.e., desiccated, and, as such, integument is wavy); posterolateral border of pronotum striate (effectively single row of anteriorly open areolae); posterior border of mesepisternum with single row of areolae, those in ventral half open anteriorly; mesepisternum with row of areolae along anterior border and ventral border, as well as in midtransverse line of upper half (fig. 4); metepisternum with borders composed of open areolae; metanotum areolate; propodeum coarsely areolate; wings clear and hyaline, veins brown.



FIGURE 3. Microphotograph of right lateral view of holotype female (JZC Bu-551) of *Archeofoenus tartaricus*, new genus and species, in Cenomanian Burmese amber.

Head broad, longer than wide, width (across compound eyes) 0.98 mm, length (to apex of clypeus) 0.78 mm; gena narrow, genal width at about midlength 0.20 mm; malar space narrow, short, length less than basal mandibular width; compound eye large, bare, prominent, ovoid, longer than wide, length 0.59 mm, width 0.35 mm, without circumocular carina, inner margins straight and parallel, interocular distance 0.65 mm; ocelli small, arranged in broad triangle on top of vertex above compound eyes, median ocellus separated from lateral ocelli by 1.5 times ocellar diameter, lateral ocelli separated by nearly 3 times their diameter and separated from ocular border by about $2.4\times$ their diameter. Antennal toruli broadly separated, situated slightly below midlength of compound eye; scape short, robust, slightly shorter than first flagellomere; pedicel short, about one-half length of scape; flagellum filiform, with 12 flagellomeres; flagellomeres each longer than wide, individual lengths $2\text{--}3\times$ their widths, lengths gradually shortening toward apex of flagellum; apicalmost flagellomere with acutely rounded apex. Clypeus short, with apical margin sinuate. Mandible short, broad, bidentate, subapical tooth broadly triangular. Maxillary and labial palpi short; labial palpus with five palpomeres; maxillary palpus with perhaps five palpomeres (four palpomeres clearly observable; short basal palpomere may be present but difficult to discern).



FIGURE 4. Microphotograph of mesosoma of holotype female (JZC Bu-551) of *Archeofoenus tartaricus*, new genus and species, in left lateral view.

Mesosoma short and high, length 1.73 mm, maximum height 1.33 mm; pronotum without defined, raised posterior dorsal surface bordering mesoscutum, posterior border broadly concave, lateral surfaces large; prothoracic spiracle covered by rounded knob on posterolateral margin of pronotum; mesoscutum without transverse carinae or striae and with anterior border broadly rounded in profile, with notauli strong, Y-shaped, and percurrent, mesoscutal length 0.98 mm; mesoscutellum arched in profile (fig. 4), medial length 0.40 mm; metanotum subvertical, short, length 0.13 mm; propodeum with distinct dorsal surface, dorsal length (between metanotum and articulation with metasomal petiole) 0.14 mm. Legs long, with slender podites; tibial spur formula 1-2-2, spurs prominent; pro- and mesotrochantelli distinct but fused to associated femora; metacoxal groove longitudinal, weakly developed; metacoxa without distal lobe; metatrochanter with dorsolateral groove; metatrochantellus present but somewhat indistinct; metafemur length 1.13 mm, metatibia length 1.15 mm; metabasitarsus elongate but shorter than combined lengths of remaining tarsomeres, metabasitarsus length 0.63 mm, lengths of remaining tarsomeres (from base to apex), 0.25 mm, 0.20 mm, 0.13 mm, and 0.13 mm; pretarsal claws small, simple; arolium small. Forewing (fig. 5A) with pterostigma much longer than wide, tapering gradually in width to acute apex, margin inside marginal cell nearly

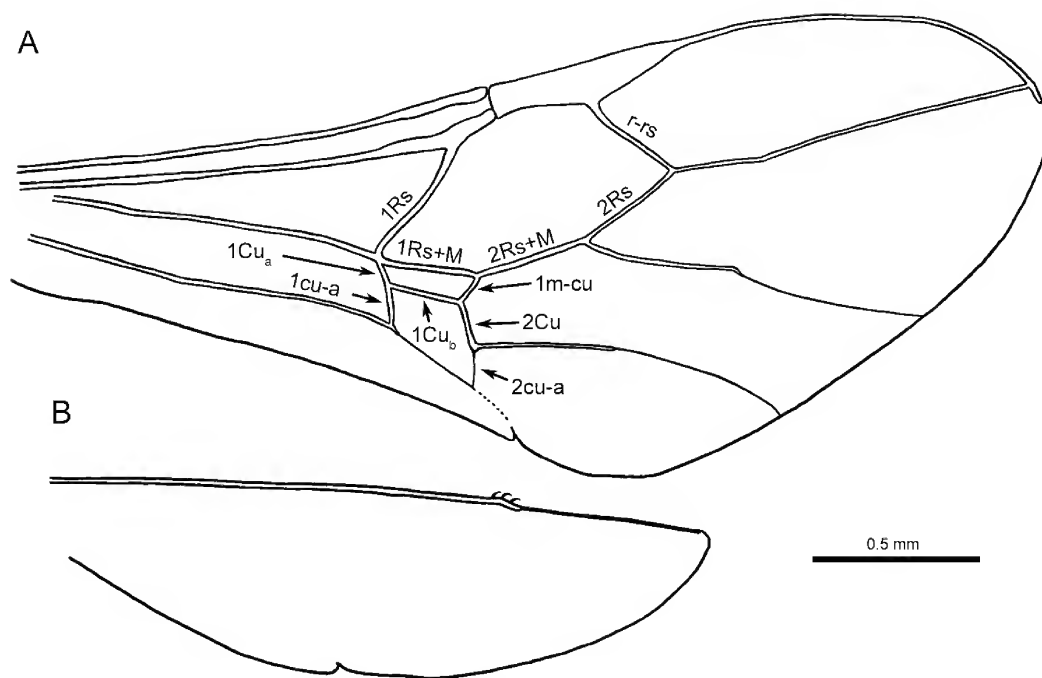


FIGURE 5. Wing venation of holotype female (JZC Bu-551) of *Archeofoenus tartaricus*, new genus and species (all to the same scale). **A.** Forewing, with pertinent veins labeled. **B.** Hind wing.

straight; M+Cu forking distad midlength of Sc+R; M+Cu fork confluent with 1Rs, with distinct 1M lacking (thus discal cell below level of M+Cu); 1Cu_a in line with 1cu-a; 1Rs+M straight, shorter than 2Rs+M; 2Rs nearly forming straight line with 2Rs+M, subequal in length to 2Rs+M; r-rs near pterostigmal midlength, elongate, as long as 2Rs; marginal cell broad, elongate, extending nearly to wing apex, with Rs comparatively straight for majority of marginal cell length; rs-m crossveins absent; discal cell narrow, with short, straight 1m-cu giving an inverted (upside down) trapezoidal shape; 2m-cu absent; 2A1 and 2cu-a present as dark infumate veins, demarcating closed subdiscal cell. Hind wing (fig. 5B) without venation except C+R, with three distal hamuli near apical termination of R; without jugal lobe.

Metasoma ovoid in profile, longer than mesosoma, length 1.5× length of mesosoma; tergum I and II fused, forming stocky, triangular petiole, petiole width at articulation with mesosoma 0.10 mm; ovipositor exserted, curved upward, thin, short, length 1.00 mm, length of sheaths 1.05 mm.

♂: Unknown.

HOLOTYPE: ♀ (fig. 3), JZC Bu-551; Cretaceous amber (Cenomanian), Myanmar, Kachin, Tanai Village on Ledo road 105 km NW of Myitkyna; Zigras collection, available through and for permanent deposition in the Division of Invertebrate Zoology, American Museum of Natural History, New York.

ETYMOLOGY: The specific epithet is taken from the Greek mythological prison of the underworld, Tartarus, and the suffix *-ikos* (*-icus*) meaning “of” or “belonging to.”

Subfamily Aulacinae Shuckard, 1841

Tribe Electrofoenini Cockerell, 1917b

Electrofoenini Cockerell, 1917b: 365. Type genus: *Electrofoenus* Cockerell, 1917b.

DIAGNOSIS: This group is distinctive relative to its nominate tribe, Aulacini Shuckard, 1841 (= extant Aulacidae, s. str., as used by most contemporary authors), distinguished by following combination of traits: large compound eyes; elongate, projecting mandibles; forewing 2Rs+M elongate; pretarsal claws exceedingly small and simple; presence of a complete occipital carina; percurrent, Y-shaped notauli; and absence of transverse carinae or striae on mesoscutum (except for prominently raised carina along anterior border) (last three traits confirmed only for new genus described herein).

INCLUDED GENERA: *Electrofoenus* Cockerell, 1917b, and *Electrofoenops*, new genus, both in Burmese amber.

Key to Genera of Electrofoenini

1. Forewing with 1cu-a confluent with M-Cu, thus no 2M+Cu present; 2m-cu meeting second submarginal cell in basal half (i.e., 2M shorter than 3M); mandible bidentate (refer to Cockerell, 1917b) *Electrofoenus* Cockerell
- Forewing with 1cu-a basal M-Cu split, thus short 2M+Cu present; 2m-cu meeting second submarginal cell slightly apical to midlength (i.e., 2M longer than 3M); mandible tridentate *Electrofoenops*, n. gen.

Electrofoenops, new genus

TYPE SPECIES: *Electrofoenops diminuta*, new species.

DIAGNOSIS: Similar to *Electrofoenus* but differs in tridentate mandible; forewing with 1cu-a basal to M-Cu split, thus producing short 2M+Cu prior to origin of 1M and 1Cu; and with 2m-cu meeting second submarginal cell slightly apical to cell's midlength such that 2M is longer than 3M.

ETYMOLOGY: The new generic name is a combination of *Electrofoenus*, type genus of the tribe, and the suffix *-ops*, meaning, "relating to appearance." The gender of the name is feminine.

Electrofoenops diminuta, new species

Figures 6–7

DIAGNOSIS: As for genus (above).

DESCRIPTION: ♀: Total length as preserved (excluding antennae and stub of ovipositor: ovipositor broken at surface of amber near its base and therefore almost entirely missing) 4.50 mm; forewing length 3.25 mm; integument largely black to dark brown (where not augmented by preservation), largely glabrous, without pronounced sculpturing or punctation (except where

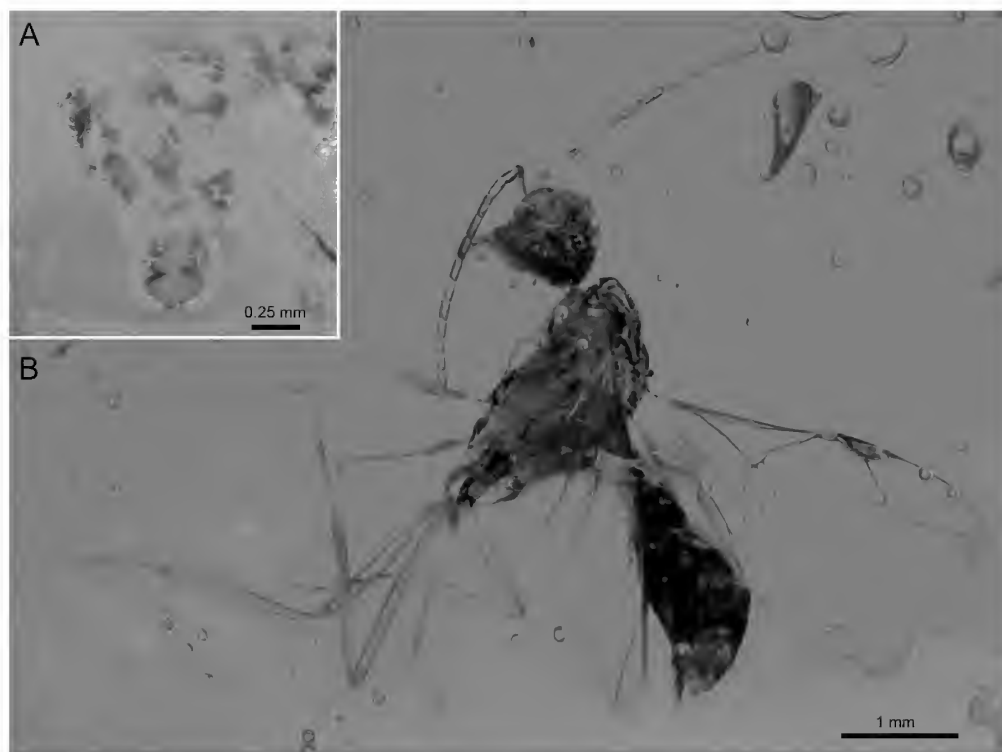


FIGURE 6. Microphotographs of holotype female (JZC Bu-60) of *Electrofoenops diminuta*, new genus and species, in Burmese amber. **A.** Facial view. **B.** Left lateral habitus.

noted below), largely faintly and finely imbricate; outer and upper surfaces of mandible, gena, and postgena with scattered, elongate, fine setae (fig. 6A); wings clear and hyaline, veins brown.

Head broad, much wider than long, width (across compound eyes) 1.05 mm, length (to apex of clypeus) 0.75 mm; occipital carina complete; gena broad but narrower than compound eye; malar space narrow, short, length much less than basal mandibular width; compound eye large, prominent, almost circular, only slightly ovoid, bare (i.e., without setae between ommatidia), without circumocular carina, inner margins parallel, compound eye length 0.55 mm, width 0.50 mm, interocular distance 0.63 mm; ocelli small, arranged in small triangle on top of vertex above compound eyes, median ocellus separated from lateral ocelli by less than one ocellar diameter, lateral ocelli separated by approximately 1.5× their diameter and from ocular border by slightly more than twice their diameter. Antennal toruli broadly separated, situated near base of clypeus and at lower tangent of compound eyes; scape robust, about 2.7× as long as pedicel, longer than first flagellomere; flagellum filiform, with 12 flagellomeres; flagellomeres each longer than wide, ranging in lengths from 1.8–2.6× individual widths except apicalmost flagellomere, which has a length 3× its width; first flagellomere slightly longer than one-half length of scape; apical flagellomere slightly longer than first flagellomere. Clypeus short, with apical margin sinuate. Mandible long, length 0.40 mm, strongly projecting (fig. 6A), outer margin in apical half broadly arched inward, tridentate (two triangular teeth along length and large apical tooth).

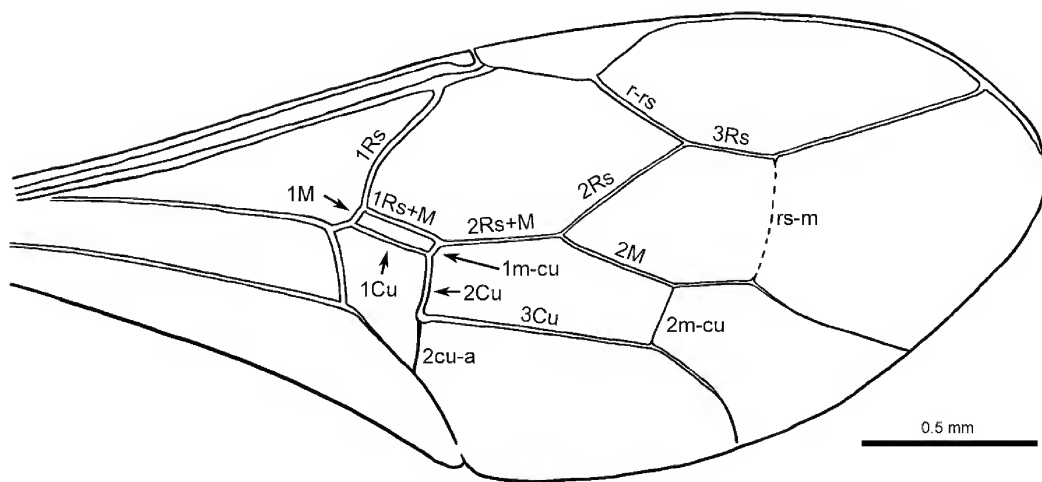


FIGURE 7. Forewing venation of holotype female (JZC Bu-60) of *Electrofoenops diminuta*, new genus and species, with pertinent veins labeled.

Mesosoma longer than high, length 1.38 mm, maximum height 1.25 mm; pronotum without defined, raised posterior dorsal surface bordering mesoscutum, posterior border broadly concave, lateral surfaces large; prothoracic spiracle covered by rounded knob on posterolateral margin of pronotum; mesoscutum without transverse carinae or striae except for prominent carina along anterior border, notauli deeply impressed and Y-shaped, mesoscutal length 0.70 mm; mesoscutellum scarcely arched in profile, medial length 0.42 mm; mesopleuron areolate ventrally, with single row of faint areolae along border with metepisternum; metanotum areolate, subvertical, short, length 0.09 mm; propodeum areolate, with prominent dorsal surface, dorsal length (between metanotum and articulation with metasomal petiole) 0.14 mm. Legs long, with slender podites; tibial spur formula 1-2-2, spurs prominent; pro- and mesotrochantelli distinct but fused to associated femora; metacoxal longitudinal groove faint; metacoxa without distal lobe; metatrochanter with dorsolateral groove; metatrochantellus present but somewhat indistinct; metafemur length 1.25 mm, metatibia length 1.30 mm; metabasitarsus elongate but shorter than combined lengths of remaining tarsomeres, metabasitarsus length 0.70 mm, lengths of remaining tarsomeres (from base to apex), 0.25 mm, 0.15 mm, 0.09 mm, and 0.10 mm; pretarsal claws small, simple; arolium minute. Forewing (fig. 7) with narrow costal space of comparatively consistent width along its length, narrower than pterostigma; pterostigma longer than wide, expanded in width medially, tapering gradually in width to acute apex, margin inside marginal cell comparatively straight; 1cu-a basad M-Cu fork, thus short 2M+Cu present prior to bifurcation of veins; 1Rs elongate, slightly arched; 1M exceedingly short, about as long as 2M+Cu and 1m-cu; 1Rs+M straight, slightly shorter than 2Rs+M; 2Rs straight, distinctly angled relative to 2Rs+M; r-rs originates at widest part of pterostigma (slightly distad pterostigmal midlength), elongate, longer than 3Rs but slightly shorter than 2Rs; marginal

cell broad, with greatest width anteroposterior breadth near rs-m, elongate, separated from wing apex by distance equal to one-half length of pterostigma; rs-m nebulous; second submarginal cell large but much smaller than massive first submarginal cell, second submarginal cell pointed basally; discal cell narrow, above level of M+Cu; 1m-cu straight and parallel to 1M; 2m-cu present but weakened (thin); 2A1 and 2cu-a present as infumate veins, enclosing subdiscal cell; subdiscal cell quite large and strongly pointed posteriorly. Hind wing without venation except C+R, with three distal hamuli near termination of R; without jugal lobe.

Metasoma ovate in profile, longer than mesosoma, length 1.5× length of mesosoma; tergum I and II fused, forming stocky, triangular petiole; ovipositor and sheaths only preserved within basal extremes (cut off at surface of amber).

♂: Unknown.

HOLOTYPE: ♀, (fig. 6B), JZC Bu-60; Cretaceous amber (Cenomanian), Myanmar, Kachin, Tanai Village on Ledo road 105 km NW of Myitkyna; Zigras collection, available through and for permanent deposition in the Division of Invertebrate Zoology, American Museum of Natural History, New York.

ETYMOLOGY: The specific epithet is derived from the Latin, *diminutus* (meaning, “lessened”), in reference to the smaller size of the species relative to *Electrofoenus gracilipes* Cockrell, 1917b.

Key to Suprageneric Groups of Aulaciformes

The following key is modified from that presented by Engel and Wang (2016), and attempts to incorporate the tribes presented above.

1. Metasomal terga I and II fused; propleura abutting dorsally for much of their length 2
 - Metasomal terga I and II separated; propleura not abutting dorsally for much of their length (Cretaceous: Russia, northern China, Mongolia, England, Spain, and New Jersey). Baissidae Rasnitsyn
- 2(1). Metasomal segment I with anterior margin almost touching metanotum; toruli never at or bordering ventral tangent of compound eyes; propodeum not pyramidal [Gasteruptiidae Ashmead] 3
 - Metasomal segment I with anterior margin distinctly separated from metanotum; toruli usually (but not exclusively) at or near ventral tangent of compound eyes; propodeum pyramidal [Aulacidae Shuckard, s.l.] 6
- 3(2). Forewing with 2m-cu and 3rs-m present; notauli percurrent, meeting transscutal sulcus, not Y- or U-shaped (Cretaceous: Myanmar). Hypselogastrinae Engel
 - Forewing with 2m-cu and 3rs-m absent; notauli not reaching transscutal sulcus, meeting medially and forming U-shaped impression. 4
- 4(3). Petiole triangular in dorsal view; propleura not elongate or necklike; metatibia not clavate (Cretaceous: Taimyria and Mongolia) Kotujellitinae Rasnitsyn
 - Petiole elongate, tubular; propleura elongate, necklike; metatibia clavate. 5

- 5(4). Mandibles short, not broadly overlapping; forewing discal cell with 1Rs+M forming node at 1Rs, M+Cu, and 1Cu, with 1M absent; female subgenital sternum slit or notched; metatrochanter with trochanteral groove; metatrochantellus usually present (Recent: worldwide) Gasteruptiinae Ashmead
- Mandibles long, broadly overlapping; forewing discal cell formed by 1Rs+M intersecting basal vein or cell absent (1Rs+M and 1Cu fused and 1m-cu absent); female subgenital sternum simple; metatrochanter with or without groove; metatrochantellus absent (Recent: Australia, New Zealand, southwestern Pacific, and South America) Hyptiogastrinae Crosskey
- 6(2). Forewing rs-m crossveins and 2m-cu absent; occipital carina present and complete [Hyptiogastritinae Engel] 7
- Forewing rs-m crossveins and 2m-cu present; occipital carina present or absent [Aulacinae Shuckard, s.l.] 8
- 7(6). Forewing with discal cell above level of M+Cu (i.e., 1M present, with 1Rs+M arising from “basal vein” and 1Cu in line with M+Cu); mesoscutum transversely carinate-striate; small wasps, less than 4 mm in length (Cretaceous: Myanmar) Hyptiogastritini Engel
- Forewing with discal cell below level of M+Cu (i.e., 1Rs+M forming node with 1Rs, M+Cu, and 1Cu, and with 1M absent) (fig. 4A); mesoscutum imbricate (confirmed only for *Archeofoenus*); moderate-sized wasps, approximately 4.5–5 mm in length (confirmed only for *Archeofoenus*) (Cretaceous: Myanmar) Archeofoenini, n. trib.
- 8(6). Mesoscutum transversely carinate; forewing 2Rs+M as long as or shorter than 1Rs+M, and shorter than 2Rs; mandibles variable (Eocene–Recent: worldwide) Aulacini Shuckard
- Mesoscutum imbricate; forewing 2Rs+M longer than 1Rs+M and as long as 2Rs; mandible elongate and projecting (Cretaceous: Myanmar) Electrofoenini Cockerell

DISCUSSION

These three species bring the total of Burmese amber Evanioidea to 12 species (table 1), encompassing the families Praeaulacidae, Othniodellithidae, Gasteruptiidae, Aulacidae, and Evaniidae. This is the greatest diversity of evanioids from any amber deposit. Admittedly, those gasteruptiids and aulacids present are not crown-group species, but they may nonetheless be included in broader concepts of their respective families. As was elaborated by Engel et al. (2016a), the Othniodellithidae are generally primitive among Evanioidea as evidenced by the large number of flagellomeres (Neoevanioidea share a reduction to 12 or fewer flagellomeres), the medially developed pronotum, and the presence of medial and transverse mesoscutal sulci. Conversely, the family possesses apomorphically elongate maxillary palpi, large squared mandibles, and a prominent facial horn. Among the basal lineages of Evanioidea there is not a clear indication of similarity to any of the Praeaulacidae or Nevaniidae, although the lack of prominent transverse striae might suggest a relationship closer to the Neoevanioidea than to either of these “paleoevanioidean” families, but the homology and polarity of such sculptural detail is unclear.

It is tempting to consider the differences between *O. mantichora* and *X. preta* in metasomal shape, mandibular dentition, flagellomere number, and head size as sexual dimorphism, and that the latter could be the male of the former. However, the distinctive differences in wing venation tend to suggest otherwise and there remains the possibility that the holotype of *X. preta* is a female (the metasomal apex is missing), although this seems unlikely. The discovery of more complete material will be needed before a conclusive decision regarding the relative importance of these characters.

None of the Aulacidae in Burmese amber can be considered as belonging to typical members of the family (i.e., crown-group Aulacini). In one manner or another, all are plesiomorphic relative to extant genera and species. Nonetheless, they exhibit at least one noteworthy synapomorphy of the family, specifically the presence of a metacoxal groove, presumably used to guide the ovipositor as in modern species. Furthermore, the pyramidal form of the propodeum is also known only in Aulacidae and may be a defining feature for the larger group. Likewise, the low position of the antennal toruli in most of the fossil species is shared with most Aulacidae, as is the presence of percurrent, Y-shaped notauli.

The genera *Hyptiogastrites*, *Protofoenus*, and *Archeofoenus* are noteworthy for the absence of the crossveins 1rs-m, 2rs-m, and 2m-cu along with the primitive retention of a complete occipital carina. *Protofoenus* and *Archeofoenus* are distinct from *Hyptiogastrites* in the low position of the discal cell (paralleling that character state found in Gasteruptiinae), and they are also larger in overall size. The former two genera are quite similar and it may prove that with the continued discovery of new material they would be better served as a united group. For now, the differences in wing venation, coloration, and mandibular form seem sufficiently different to recognize them as separate genera. In contrast to all these genera, *Electrofoenus* and *Electrofoenops* both have the more typical wing venation of Aulacidae, with the presence of 2m-cu and at least one rs-m crossvein. Nonetheless, *Archeofoenini* and *Electrofoenini* have mesoscuta lacking the transverse striae so distinctive among crown-group Aulacinae. At the most, the type species of *Electrofoenops* has a prominent anterior carina, but no other sculpturing across the mesoscutal surface. Cockerell (1917b) asserted in his brief description of *Electrofoenus* that the wings were plicate, a prominent feature of Gasteruptiidae not found in any Aulacidae. Whether he correctly interpreted this trait remains to be confirmed, and there is really no evidence that his species is more closely allied to the gasteruptiids, particularly when taken in the light of *Electrofoenops*.

As more Cretaceous Evanioidea are progressively described, particularly those from the rich amber sources of Myanmar and Spain, it will be fascinating to see whether they aid attempts to resolve distinctions between the families Gasteruptiidae and Aulacidae (Turrisi et al., 2009). Already our few glimpses into the considerable diversity of Mesozoic Evanioidea reveal a fauna much more varied than is present today, and it is among the paleoevanioids that we might obtain the greatest clarity into the phylogenetic placement of Evanioidea as a whole among other evaniomorphan Apocrita. From the little data available, it at least appears as though evanioids first diverged during the Upper Jurassic and that by the earliest Cretaceous sufficient cladogenesis had transpired such that stem-group Evaniiformes and Aulaciformes were already present. Many of these stem groups persisted throughout much of the Cretaceous, but by the Cenozoic only crown-group Evaniidae,

Gasteruptiidae, and Aulacidae remained. This outline is helpful at the least for providing calibration points in estimates of divergence times, but reveals little about those important biological transitions (e.g., host shifts) going on during the considerable biotic and climatic changes of the Cretaceous.

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APPENDIX

FAMILY-GROUP NAMES AMONG EVANIOIDEA

There has been considerable confusion regarding the first usage of some family-group names for evanioid wasps and it is therefore appropriate to provide a tabulation of nomenclatural details for these. Presently there are 20 available family-group names among Evanioidea, and the apparent earliest establishment of these is provided. The format for the material is based on those family-group summations presented by Engel (2005), Engel and Krishna (2004), and Engel and Haas (2007).

1. Evaniales Latreille, 1802: 328. Type genus: *Evania* Fabricius, 1775. Combining stem: Evani-.
2. Foenidae Kirby, 1837: 258, *nomen suppressum*. Type genus: *Foenus* Fabricius, 1798. Combining stem: Foen-. Note: As discussed by Crosskey (1962), this name may be considered suppressed relative to Gasteruptiidae Ashmead, 1900, under Article 40.2 of the ICZN (1999). Following Recommendation 40A (ICZN, 1999), the latter name would be considered as “Gasteruptiidae Ashmead, 1900 (1837),” for nomenclatorial purposes.
3. Aulacidae Shuckard, 1841: 121. Type genus: *Aulacus* Jurine, 1807. Combining stem: Aulac-. Note: It is interesting that Shuckard appears to have also been the first to establish the family Megalyridae within this same paper (Shuckard, 1841: 119), a group more widely attributed to Schletterer (1889).

4. Gasteruptioninae Ashmead, 1900: 7, *nomen imperfectum* (recte Gasteruptiidae, refer to Schulz, 1906: 133) et *nomen protectum* (ICZN, 1999: Art. 40.2) Type genus: *Gasteruption* Latreille, 1796. Combining stem: Gasterupti-. Note: This name is to be considered protected from priority in relation to Foenidae Kirby, 1837; refer to note under that name.
5. †Electrofoenini Cockerell, 1917b: 365. Type genus: †*Electrofoenus* Cockerell, 1917b. Combining stem: Electrofoen-.
6. Hyptiogastrinae Crosskey, 1953: 351. Type genus: *Hyptiogaster* Kieffer, 1903. Combining stem: Hyptiogastr-.
7. †Praeaulacidae Rasnitsyn, 1972: 70. Type genus: †*Praeaulacus* Rasnitsyn, 1972. Combining stem: Praeaulac-.
8. †Cretevaniidae Rasnitsyn, 1975: 83. Type genus: †*Cretevania* Rasnitsyn, 1975. Combining stem: Cretevani-. Note: This group is considered a junior subjective synonym of Evaniidae.
9. †Kotujellidae Rasnitsyn, 1975: 87, *nomen invalidum* (ICZN, 1999: Art. 39). Type genus: †*Kotujella* Rasnitsyn, 1975, *nomen praeoccupatum* (nec *Kotujella* Andreeva, 1962). Combining stem: Kotujell-. Note: The preoccupied generic name was replaced by *Kotujellites* Rasnitsyn in Pagliano and Scaramozzino, 1990, while the family-group name was replaced by Kotujellitinae Rasnitsyn, 1991.
10. †Anomopterellidae Rasnitsyn, 1975: 88. Type genus: †*Anomopterella* Rasnitsyn, 1975. Combining stem: Anomopterell-.
11. †Baissidae Rasnitsyn, 1975: 90. Type genus: †*Baissa* Rasnitsyn, 1975. Combining stem: Baiss-.
12. †Manlayinae Rasnitsyn, 1986: 156. Type genus: †*Manlaya* Rasnitsyn, 1980. Combining stem: Manlay-. Note: This group is considered a junior subjective synonym of Baissidae.
13. †Cretocleistogastrinae Rasnitsyn, 1990: 189. Type genus: †*Cretocleistogaster* Rasnitsyn, 1975. Combining stem: Cretocleistogastr-.
14. †Kotujellitinae Rasnitsyn, 1991: 131, *nomen novum pro* Kotujellidae Rasnitsyn, 1975. Type genus: †*Kotujellites* Rasnitsyn in Pagliano and Scaramozzino, 1990, *nomen novum pro* *Kotujella* Rasnitsyn, 1975. Combining stem: Kotujellit-.
15. †Andreneliidae Rasnitsyn and Martínez-Delclòs, 2000: 77. Type genus: †*Andrenelia* Rasnitsyn and Martínez-Delclòs, 2000. Combining stem: Andreneli-.
16. †Hyptiogastritinae Engel, 2006: 454. Type genus: †*Hyptiogastrites* Cockerell, 1917a. Combining stem: Hyptiogastrit-.
17. †Nevaniinae Zhang and Rasnitsyn, 2007: 150. Type genus: †*Nevania* Zhang and Rasnitsyn, 2007. Combining stem: Nevani-.
18. †Othniodellithidae Engel and Huang in Engel et al., 2016a: 123. Type genus: †*Othniodellitha* Engel and Huang in Engel et al., 2016a. Combining stem: Othniodellith-.
19. †Hypselogastrinae Engel in Engel and Wang, 2016: 179. Type genus: †*Hypselogastrion* Engel in Engel and Wang, 2016. Combining stem: Hypselogastr-.
20. †Archeofoenini Engel, herein: 11. Type genus: †*Archeofoenus* Engel, herein. Combining stem: Archeofoen-.